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ADAPTATION THROUGH NATURAL SELECTION AND ORTHOGENESIS[1]

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Mr. President, Members of the Society, and Friends: When the president of our society, Professor Conklin, asked me to open this discussion, he suggested that I speak in advocacy of natural selection as the dominant factor in adaptation, saying that several speakers would follow who would attack this conception. As I understand it, a paper in advocacy of natural selection is desired not so much that it may be a target at which following speakers may direct their shafts, as that this conception may not stand without defenders.

It involves some temerity to speak to an audience of American naturalists upon natural selection, for the conception is more than a decade old. It dates even from the dark ages of the middle of the last century, and we naturalists, like the Athenians to whom Paul spoke, are continually seeking some new thing. I can not even, as DeVries and Bateson in the case of Mendel's principles, claim the honor of a re-discoverer, for through all the years since its first promulgation the conception of natural selection has been constantly to the fore and has been discussed and re-discussed until many, I fear, have wearied of it, and for this very reason may be ready to give too undiscriminating welcome to other conceptions that seek to supplant the old idea.

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[1] Read at the Symposium on Adaptation at the meeting of the American Society of Naturalists, Cleveland, January 2, 1913.

There are two sets of factors in producing and determining the direction of evolution, those within the organism, and those external to it. In earlier studies of evolution the external factors received by far the most attention, and only recently have the internal factors begun to receive the thought they deserve. Of the external factors, natural selection is the one for which the largest claims have been made and the one whose claims have been most cordially allowed. I think, however, there are few, if any, of us who do not feel that some of the advocates of natural selection have gone too far. Wallace, for example, would not allow that there are any characters of animals or plants which are not useful to their possessors and have not been perpetuated and emphasized because of this usefulness. Admitting, as we must, that we know but little of the intimate life of organisms, and that the use of many really most useful characters may fail to impress us only because of our ignorance of real conditions, still I think most of us feel not only that the claim that all structures and qualities of organisms are useful is an exaggerated claim, but that very many characteristics are either of indifferent quality, or are so slightly useful as not to be of selection value, or even are slightly disadvantageous. The more closely one studies any organism the more will he become impressed with the number of these non-useful or doubtfully useful qualities, and close and careful students are likely to find their vision of natural selection grow dim, like the pilgrim who, in the midst of the woods, could not see the forest for the trees.

But as we view organic nature in its wider aspects is there any other feature so prominent as the adaptation of organisms to their environment and to the lives they must live in the midst of this environment? However many details of structure or behavior may fail to show their utility, still it remains true that there is no phenomenon of organic nature more impressive than adaptation.

In our study of evolution we have, then, this thing to explain—namely, the universal prevalence of a high degree of adaptation of organisms in habit, function and structure, to their environment, and yet the presence of many qualities, for the most part minor qualities, which so far as we can judge, are non-adaptive. I would suggest for your consideration the propositions that the broader adaptive features are due to natural selection, and that the non-adaptive minor characters are the result partly of factors within the organism, and partly of external factors other than natural selection. This paper will not refer further to these other external factors, but will discuss one of the factors within the organism.

Evidence accumulated during the last decade seems to indicate that fluctuating variations are not significant, and that only mutations are stable and can serve as a foundation for evolution. Perhaps we have accepted this statement a little too hastily. The actual evidence in its favor is not all that could be desired, but it seems to be the general opinion to-day. If this opinion is well founded, it is through the study of the origin and nature of mutation that we may hope to gain most light upon the problem of the origin of adaptation.

When one comes to think of it, we really know very little of mutation. Few instances have been carefully observed and recorded. But in the midst of this scant knowledge of mutation one fact stands out clearly, that mutation apparently is not indeterminate, occurring in all directions equally, and changing from generation to generation, as would be the case were it purely fortuitous. Our best studied instances of mutation are still seen in *Œnothera lamarckiana,* and in all the observations upon the mutation of this species nothing is more patent than that there are certain definite tendencies for particular mutants of very complex and very clearly recognizable types to appear generation after generation, in numbers that are very much greater than could be accounted for by any chance aggregation of unit characters to make these few well-marked types.

In 1905 I wrote as follows:

> In the Amsterdam Garden the mutant *albida* appeared in four different generations from *lamarckiana* parents, previous to 1902, 15 *albida* appearing in one generation, 25 in another, 11 in another and 5 in another. *Nanella* appeared 5 times in one generation, and in other

generations, respectively, 3, 60, 49, 9, 11 and 21 times. *Lata, oblonga, rubrinervis* and *scintillans* appeared frequently.

In the fourth generation, along with 14,000 *lamarckiana* plants, there appeared 41 *gigas,* 15 *albida,* 176 *oblonga,* 8 *rubrinervis,* 60 *nanella,* 63 *lata* and 1 *scintillans,* all bred from *lamarckiana* seed. In the fifth generation, similarly bred from pure *lamarckiana* seed, among 8,000 *lamarckiana* plants were found 25 *albida,* 135 *oblonga,* 20 *rubrinervis,* 49 *nanella,* 142 *lata* and 6 *scintillans.* In the fourth generation one plant in 80 was *oblonga.* In the fifth generation one plant in 60 was *oblonga.* DeVries himself says: "A species therefore, is not born only a single time, but repeatedly, in a large number of individuals and during a series of consecutive years.

Oblonga differs from the parent species *lamarckiana* not in a single feature, but in an elaborate complex of characters. The other mutants likewise are distinguished from *lamarckiana* by a complex of characters rather than by a single feature.

The mutation can hardly be entirely fortuitous if, for several generations, out of every thousand offspring of pure *lamarckiana* parents, there appear more than ten plants marked by the particular complex group of characters which designate *oblonga.* Were *oblonga* demarcated from *lamarckiana* by but a single character, it would be remarkable to find it appearing repeatedly and in such numbers. When we remember that it is defined by an extensive series of characters differentiating it from *lamarckiana* and from all other mutants observed, are we not led to the conclusion that mutation in *Œnothera lamarckiana* is not wholly fortuitous, but is to a degree predetermined; and that there is some tendency to the production of the *oblonga* and other types in numbers much greater than would be secured by purely fortuitous and indeterminate mutation?

Mutation in our most carefully observed instance, therefore, is clearly determinate. There is in *Œnothera lamarckiana* a tendency to mutate in certain definite directions generation after generation. This trend to mutation in certain particular directions is an example of a condition within the organism which might decidedly affect the course of the future evolution of this *Œnothera* and its descendants.

But we can safely go further. Not only have we evidence that there exist tendencies to produce certain mutants repeatedly, paleontological records show, I believe, that there have existed trends toward an increasing emphasis upon certain characters and that these trends, in some instances at least, lay along lines that produced no more perfect adaptation of their possessors to their environment.

Neumayr's well-remembered figures of fossil *Paludinas* from Slavonian lake deposits show an increasing rugosity of shell and irregularity of aperture, but the separate steps of this change could hardly have been of selection value and have occurred under the control of natural selection. One is irresistibly drawn to believe that there was in these *Paludinas* an internal tendency to mutate from generation to generation toward increasing rugosity of the shell and increasing irregularity of its aperture.

Similar trends in the development of limb and tooth structure of the horse were long ago emphasized by American paleontologists. There is no conceivable utility in the modified shell form of the *Paludina,* and, in the case of the horse, the wonder is that the race has not long ago been exterminated. Among the Cephalopods are some forms which show most complex patterns of the partitions. There are complete intergrading stages shown in the known species between simple suture lines and the most fantastically fimbriated. There seems here, again, to be evidence of a trend toward increasing convolution of the sutures, rather than evidence of the appearance of a useful character and its increase by successive steps each of selection value. In a somewhat similar way, over-ornamentation and bizarre character developed in the Trilobites by steps which can hardly be imagined useful. Many such examples might be cited.[2]

It may seem that I am arguing against the importance of natural selection, but I think I am not, and for this reason: the very trends, of whose existence I think we have good evidence, are themselves subject to natural selection, and if they are in hurtful directions, they will ultimately cause the extermination of the species exhibiting them. I very much doubt if such a monstrosity as the horse could long persist, except for man's aid, for it

[2] On the afternoon of the day when this paper was read Professor B. M. Davis reported that among the offspring of his *Œnothera* hybrids were some mutants with flowers larger than either parent species, and that for two generations (as far as his experiments went) the flowers increased in size. This is apparently an example of just such a trend in mutation as I have indicated above.

is about the least adaptable beast we know. The Cephalopods with complex partitions have all perished. The bizarre Trilobites similarly persisted each for but a brief period.

I would not claim that the over-ornamentation in these cases was the cause of extermination. It seems more probable that it is merely one noticeable indication of a general unbalanced condition of the organism, a condition affecting probably function as well as structure. I suspect that more species have perished because of physiological maladjustment than from any disadvantageous structural qualities.

In quatenary times in numerous species, great emphasis seems to have been laid upon bulk and the very hugeness of some of these species probably aided in their extermination.

Non-adaptive qualities, when first appearing, may often be comparatively harmless, at least may not be sufficiently hurtful to lead to the extermination of the species in which they appear. But qualities comparatively innocent in their beginnings, when over-emphasized by such trends as we are discussing, may go beyond the limit that even long suffering nature will allow and extermination follow. The goblin of natural selection will get him in the end if he doesn't watch out. It is a case of giving the species rope enough and letting it hang itself. Instead, therefore, of supplanting natural selection, such orthogenesis as this really acts in the end to aid in eliminating many species whose characters in their beginnings were indifferent, natural selection finally dominating and compelling adaptation.

Since mutation-trends in helpful directions will be aided by selection, through the destruction of the rivals of their possessors, while hurtful trends will cause extermination, we see that natural selection has a determinative influence upon the direction of evolution, steering the species along safe paths of progress.

Further advance in the study of the method of evolution may be expected from the study of trends in mutation. Such study should be continued for many years, breeding in great numbers for many generations from some highly mutating stock. Such work can not well be undertaken by a single individual, for it should continue through several human generations. It should be undertaken by some institution which will ensure the endurance of the investigation beyond the present generation. Possibly the best object for such study would be the Syracuse Trilliums—*Trillium grandiflorum*—whose remarkable variation Britcher[3] has so well described. Variation in these Syracuse Trilliums is more universal and more extensive than in any other plants or animals I know. It is so great that it can hardly be of the fluctuating type. It is, in all probability, true mutation, and if so it offers the best opportunity I know for the study of the phenomena of mutation.

SUMMARY

Organisms show adaptation in their more important characters, while many of their minor characters fail to show their utility.

There are definite tendencies to mutation in particular directions, and there is abundant paleontological evidence of trends toward increasing modification in particular directions.

Qualities so appearing may be indifferent in their beginnings, but may through this orthogenesis become sufficiently useful or hurtful to affect selection. Such trends, when they affect physiological qualities, are likely to bring about an unbalanced, distorted physiological condition and be peculiarly hurtful. Probably this has been one of the chief causes of the disappearance of species.

Orthogenesis as thus interpreted is but the handmaiden of natural selection which, acting upon all qualities thus developed to major proportions, will cause them to disappear if ill-adapted. At the same time advantageous trends will be encouraged in the struggle for existence and the direction of evolution be turned toward further adaptation.

Adaptation is the most salient result of evolution and natural selection its great cause.

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[3] H. W. Britcher.